J Arid Land
https://doi.org/10.1007s40333-019-0052-3





Effects of spring fire and slope on the aboveground biomass, and organic C and N dynamics in a semi-arid grassland of northern China

ZHAO Xiang¹, HU Shuya², DONG Jie³, REN Min¹, ZHANG Xiaolin¹, DONG Kuanhu¹, WANG Changhui^{2*}

¹ College of Animal Science and Veterinary Medicine, Shanxi Agricultural University, Taigu 030801, China;

Abstract: The aboveground primary production is a major source of carbon (C) and nitrogen (N) pool and plays an important role in regulating the response of ecosystem and nutrient cycling to natural and anthropogenic disturbances. To explore the mechanisms underlying the effect of spring fire and topography on the aboveground biomass (AGB) and the soil C and N pool, we conducted a field experiment between April 2014 and August 2016 in a semi-arid grassland of northern China to examine the effects of slope and spring fire, and their potential interactions on the AGB and organic C and total N contents in different plant functional groups (C₃ grasses, C₄ grasses, forbs, Artemisia frigida plants, total grasses and total plants). The dynamics of AGB and the contents of organic C and N in the plants were examined in the burned and unburned plots on different slope positions (upper and lower). There were differences in the total AGB of all plants between the two slope positions. The AGB of grasses was higher on the lower slope than on the upper slope in July. On the lower slope, spring fire marginally or significantly increased the AGB of C₃ grasses, forbs, total grasses and total plants in June and August, but decreased the AGB of C4 grasses and A. frigida plants from June to August. On the upper slope, however, spring fire significantly increased the AGB of forbs in June, the AGB of C3 grasses and total grasses in July, and the AGB of forbs and C4 grasses in August. Spring fire exhibited no significant effect on the total AGB of all plants on the lower and upper slopes in 2014 and 2015. In 2016, the total AGB in the burned plots showed a decreasing trend after fire burning compared with the unburned plots. The different plant functional groups had different responses to slope positions in terms of organic C and N contents in the plants. The lower and upper slopes differed with respect to the organic C and N contents of C3 grasses, C4 grasses, total grasses, forbs, A. frigida plants and total plants in different growing months. Slope position and spring fire significantly interacted to affect the AGB and organic C and N contents of C₄ grasses and A. frigida plants. We observed the AGB and organic C and N contents in the plants in a temporal synchronized pattern. Spring fire affected the functional AGB on different slope positions, likely by altering the organic C and N contents and, therefore, it is an important process for C and N cycling in the semi-arid natural grasslands. The findings of this study would facilitate the simulation of ecosystem C and N cycling in the semi-arid grasslands in northern China.

Keywords: aboveground biomass; plant functional group; spring fire; slope position; N content; organic C content; semi-arid grassland

Citation: ZHAO Xiang, HU Shuya, DONG Jie, REN Min, ZHANG Xiaolin, DONG Kuanhu, WANG Changhui. 2019. Effects

Received 2017-11-26; revised 2018-06-28; accepted 2018-07-07

² State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China;

³ Beijing Institute of Science and Technology Information, Beijing 100044, China

^{*}Corresponding author: WANG Changhui (E-mail: wangch@ibcas.ac.cn)

[©] Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Science Press and Springer-Verlag GmbH Germany, part of Springer Nature 2019

of spring fire and slope on the aboveground biomass, and organic C and N dynamics in a semi-arid grassland of northern China Journal of Arid Land, 11(2): 267–279. https://doi.org/10.1007/s40333-019-0052-3

1 Introduction

Fire plays an important role in grassland ecosystems, which can affect the plant species characteristics (Satterthwaite et al., 2002; Menges and Quintana-Ascencio, 2004; Zhou et al., 2011), community structure and species diversity (Whelan, 1995; Bond and Van Wilgen, 1996). All of these might be related to biomass production and litter accumulation (Whelan, 1995; Bond and Van Wilgen, 1996). Plant species differ in their tolerance to fire as well as in their capacity to recover after being exposed to fire (Wan et al., 2001). The occurrence frequency of fire can considerably influence the structure and function of the vegetation in an ecosystem (Moreira, 2000; Saito et al., 2014). As an anthropogenic or natural disturbance, fire affects the ecosystem processes by removing the aboveground standing crop and standing litter (Blair, 1997; Knapp et al., 1998), and by increasing the nutrient contents (such as carbon (C) and nitrogen (N)) of the surface soil (Wan et al., 2001). For shorter species, its growth might be hampered in the case of high aboveground biomass (AGB) and litter production associated with it (Kaye et al., 2001; Morrison, 2002). The removal of aboveground portion by fire may cause an immediate change in the penetration of light and result in a higher soil temperature in the middle of the day (Knapp and Seastedt, 1986; Liu et al., 2007), which could promote plant growth (Tilman, 1993; Schaffers, 2002). Therefore, it is important to study how fire would affect the AGB, and N and C dynamics by changing the functional groups (for example, C₃ and C₄ plant species) and abiotic factors (such as soil temperature and moisture).

The effects of fire on the aboveground primary production and nutrient availability have been documented in detail in the literature (e.g., Blair, 1997; Barbosa and Fearnside, 2005). Plant communities differ considerably in their responses to fire (Kaye et al., 2001). The positive effect of fire on the plant biomass was observed in different grassland ecosystems (Safford and Harrison, 2004; Brys et al., 2005). Moreover, high rates of primary production may lead to the accumulation of C in the plants (Liu et al., 2007). In a grassland ecosystem, fire might also directly reduce the AGB and the stored C (Vargas et al., 2008), and change the plant coverage (Wahren et al., 2001; Vijayakumar et al., 2016). However, no consensus is reached in the responses of plant communities to fire for grassland ecosystems. Therefore, more studies are needed, especially in the semi-arid region of northern China where the grassland ecosystems are fragile, to improve our understanding of the effects of fire on the vegetation and to better manage the ecosystems.

Regional spatial heterogeneity in phenology could cause variability in the diversity of species and AGB (Vitousek et al., 1994; Röver and Kaiser, 1999; Corre et al., 2002; Shaukat et al., 2014). The topography of a region may affect the spatial distribution of soil moisture, temperature and organic matter (Burke et al., 1999; Hook and Burke, 2000; Riihimäki et al., 2017). There are several researches on the effects of topography on the ecosystem functioning, community structure and species composition in the tallgrass prairies (Abrams and Hulbert, 1987; Benning and Seastedt, 1995; Hartnett et al., 1996; Bennie et al., 2006) and shortgrass steppes (Burke et al., 1999) of North America. In the shortgrass steppes, the grass biomass is high on the lower slope, while the density of forbs is high on the upper slope (Hook and Burke, 2000; Guo, 2001). The variations in species diversity and biomass with changing slope could be explained by the differences in soil temperature (Bennie et al., 2006), soil moisture (Rowe, 1984), and available nutrients (Reynolds et al., 2007).

Instances of occurrence of fire throughout the tropics, including the savannas and tropical forests, are well documented (Abrams and Hulbert, 1987; Blair, 1997; Brys et al., 2005; Cianciaruso et al., 2010). In the semi-arid grasslands of northern China, there is little standing crop on the ground because of overgrazing in recent years, and a few studies have indicated the effects of fire on soil respiration, microbial biomass, and N transformations in these systems (Liu et al., 2007; Xu and Wan, 2008; Zhou et al., 2011). Studies on the effects of fire (especially spring fire) on the AGB, and organic C and N dynamics are also scarce. In the present study, we examined the variations of

ZHAO Xiang et al.: Effects of spring fire and slope on the aboveground biomass, and organic C and N...

AGB and the dynamics of organic C and N contents in the plants after spring fire on different slope positions (i.e., lower and upper) of a semi-arid grassland in northern China. The study addressed the following two questions: (1) how different plant functional groups (C₃ grasses, C₄ grasses, forbs, *Artemisia frigida* plants, total grasses and total plants) respond to spring fire on the upper and lower slopes?; and (2) what is the main reason that is responsible for the differences in AGB and organic C and N contents in the plants of different functional groups on the upper and lower slopes? To this end, we explored the spatial-temporal variations in the AGB and organic C and N contents of each plant functional group on both the lower and upper slopes.

2 Materials and methods

2.1 Study area and experimental design

The study was carried out in a semi-arid grassland in Youyu County (112°19′40″N, 39°59′49″E), Shanxi Province, northern China. The mean annual precipitation is approximately 434 mm, and the annual mean temperature is 4.7°C, with the values ranging from –14.0°C in January to 20.5°C in July. The soil type is chestnut soil in the Chinese classification system and calcic–orthic aridisol in the US soil taxonomic classification system. Before the experiment, *Stipa krylovii* and *A. frigida* were the dominant plant species at the study site. Other plant species, such as *Elymus dahuricus*, *Gagea pauciflora*, *Cleistogenes squarrosa* and *Salsola collina*, were also distributed.

The experiment was started in 2014 on a south-facing slope, which exhibited homogeneous soil conditions and vegetation characteristics. We established 12 plots (6 plots for burning treatment and 6 plots for control treatment) on the upper slope and 12 plots (6 each for the burning treatment and control) on the lower slope, with the size of 8 m×8 m for each plot. The altitude difference between the upper and lower slopes was 20 m. These plots were referred to as ULS, BLS, UUS and BUS, corresponding to unburned plot on the lower slope, burned plot on the lower slope, unburned plot on the upper slope and burned plot on the upper slope, respectively. For the lower or upper slope, the burned and unburned plots were arranged on the east and west sides, which were separated by a 2-m walkway. During the period from April 2014 to August 2016, the burned plots, enclosed by metal barriers, were subjected to spring fire in April once a year. All the aboveground plant parts were burned by the fire.

2.2 Plant sampling and measurements

The AGB was harvested in the mid-August in 2014, 2015, and 2016 by clipping 1 m×1 m quadrat in each plot in both the burned and unburned plots on the lower and upper slopes. In each plot, the samples were segregated by species and harvested from 6 randomly distributed quadrats with an area of 1 m×1 m for each. The plant samples were oven-dried at 65°C for 48 h and then weighed to determine the AGB. Each sample was grounded twice and passed through a 0.6-mm sieve to analyze the organic C content (%) and total N content (%).

The C₃ grasses, C₄ grasses, forbs and *A. frigida* plants were randomly collected from the 6 burned and 6 unburned plots on the lower (upper) slope from June to August in 2014 to examine the effects of spring fire on the nutrients in these different plant functional groups. The organic C and N contents for each plant functional group (C₃ grasses, C₄ grasses, forbs and *A. frigida* plants) were calculated in the burned and unburned plots on the lower and upper slopes. The organic C and N contents of all grasses were respectively calculated by adding the organic C and N contents of C₃ and C₄ grasses; and the total organic C and N contents were the sum of corresponding organic C and N contents in the C₃ and C₄ grasses, forbs and *A. frigida* plants. There were 6 repeats for the measurements of organic C and N contents. Totally, 288 samples (3 years×2 treatments (burned and unburned)×2 slope positions (upper and lower)×4 plant functional groups (C₃ grasses, C₄ grasses, forbs and *A. frigida* plants)×6 replicates) were used for determining the organic C and N contents for different plant functional groups.

The organic C content in the plant was measured using the potassium dichromate-vitriol oxidation method (Lavian et al., 2001), and the total N content in the plant was measured using the Kjeldahl digestion method (Cabrera and Beare, 1993).

2.3 Statistical analyses

We performed the analysis of variance (ANOVA) for a three-factorial design using SPSS 11.5 software (SPSS Institute Inc., Cary, NC, USA) and variance decomposition method (Ma et al., 2001) to evaluate the effects of sampling year, slope position, burning treatment, and their interactions on the AGB and dynamics of C and N contents in the plants.

3 Results

3.1 Effects of slope and spring fire on the AGB

Slope position was observed to have different effects on the AGB of C_3 grasses, forbs, C_4 grasses and A. frigida plants, on the AGB of all grasses, and on the total AGB during the growing season from June to August (Fig. 1). There was a significant difference in the AGB of C_4 grasses between the lower and upper slopes in June (P<0.01; Fig. 1c). The AGB values of C_3 grasses (P<0.01; Fig. 1a), A. frigida plants (P<0.10; Fig. 1d) and total grasses (P<0.01; Fig. 1e) were marginally or significantly higher on the lower slope than on the upper slope in July. Moreover, in August, the AGB values of C_3 grasses, A. frigida plants and total grasses on the lower slope were significantly higher than those on the upper slope (P<0.01; Figs. 1a, d and e).

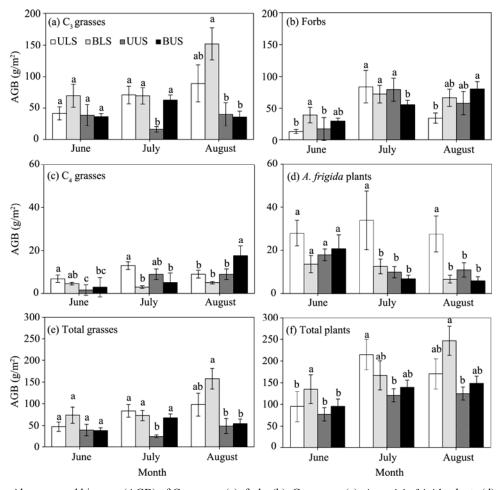


Fig. 1 Aboveground biomass (AGB) of C₃ grasses (a), forbs (b), C₄ grasses (c), *Artemisia frigida* plants (d) and all grasses (e), and total AGB of all plants (f) in June, July and August of 2014 in the burned and unburned plots on the lower and upper slopes. ULS, BLS, UUS and BUS, correspond to unburned plot on the lower slope, burned plot on the lower slope, unburned plot on the upper slope and burned plot on the upper slope, respectively. Bars mean standard errors. Different lowercase letters indicate significant differences of AGB among the plots at *P*<0.05 level in the same sampling month.

On the lower slope, spring fire significantly increased the AGB of forbs (P<0.05; Fig. 1b) and all grasses (P<0.01; Fig. 1f) in June. No significant differences were found among the AGB values of C₃ grasses, C₄ grasses, A. frigida plants and total grasses in the burned and unburned plots (P>0.05; Figs. 1a, c, d and e). However, compared with the unburned plots in June, the AGB of C₃ grasses and total grasses in the burned plots increased by 40% and 35%, respectively (Figs. 1a and e). The AGB values of C₄ grasses and A. frigida plants were 55% and 108% lower in the burned plots than in the unburned plots in June, respectively (Figs. 1c and d). These results suggested that spring fire had different effects on the AGB of different plant functional groups during the early growing season. Spring fire significantly decreased the AGB of A. frigida plants in July (P<0.01) and August (P<0.05) on the lower slope (Fig. 1d). The AGB values of C₃ grasses, forbs and total grasses, as well as the total AGB of all plants were higher in the burned plots than in the unburned plots in August (Figs. 1a, b, e and f).

On the upper slope, compared with the unburned plots, spring fire in the burned plots significantly increased the AGB of C_3 grasses (P<0.01; Fig. 1a) and total grasses (P<0.01; Fig. 1e) by 75% and 63% in July, respectively. Spring fire also significantly increased the AGB of C_4 grasses in August (P<0.05; Fig. 1b) and the AGB of forbs in July (P<0.05; Fig. 1c). However, the AGB showed an increasing trend after the burning for all plant functional groups except for A. frigida plant group (P>0.05; Fig. 1d). As shown in Figure 2, spring fire exhibited no significant effect on the total AGB of all plants on the lower and upper slopes in 2014 and 2015. Furthermore, in 2016, the total AGB in the burned plots showed a decreasing trend after fire burning compared with the unburned plots.

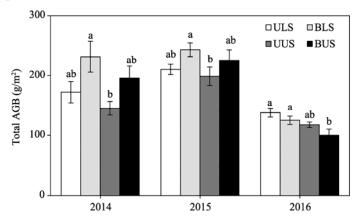


Fig. 2 Total AGB of all plants in the burned and unburned plots on the lower and upper slopes in 2014, 2015 and 2016. Bars mean standard errors. Different lowercase letters indicate significant differences of total AGB among the plots at *P*<0.05 level in the same sampling year.

3.2 Effects of slope and spring fire on the organic C content of different plant functional groups

The organic C contents of C_3 grasses, forbs, C_4 grasses, A. frigida plants and total grasses, and the total organic C content of all plants differed with slope positions in the different growing months (Fig. 3). In June, the organic C content of C_4 grasses was significantly higher on the lower slope than on the upper slope (P<0.05; Fig. 3c). For C_4 grasses, no significant differences in the organic C content were found between slope positions in July and August. The organic C content in the unburned plots showed significant differences in the C_3 grasses (P<0.01; Fig. 3a), marginal differences in the A. frigida plants (P<0.10; Fig. 3d) and significant differences in all plants (P<0.05; Fig. 3f) between the lower and upper slopes in July. Spring fire significantly decreased the organic C content of C_4 grasses on the lower slope in July and of A. frigida plants on the upper slope in July and August by 286%, 187% and 244%, respectively (P<0.05; Figs. 3c and d).

On the lower slope, spring fire significantly increased the organic C content of forbs in June (P<0.05; Fig. 3b). It also significantly decreased the organic C content of C₄ grasses in June

(P<0.001) and July (P<0.05); Fig. 3c), and of A. frigida plants in August (P<0.05); Fig. 3d). Compared with the unburned plots, there was an increasing trend in the organic C contents of C_3 grasses, forbs and total grasses, as well as the total organic C content of all plants in August in the burned plots (Figs. 3a, b, e and f). On the upper slope, spring fire significantly increased the organic C contents of C_3 grasses and total grasses by 108% (P<0.01); Fig. 3a) and 178% (P<0.01); Fig. 3e), respectively, in July. No significant differences were found among the other plant functional groups during the growing season.

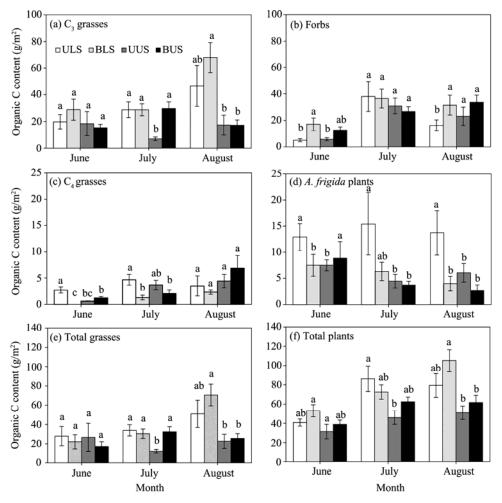


Fig. 3 Organic C contents of C_3 grasses (a), forbs (b), C_4 grasses (c), A. frigida plants (d) and total grasses (e), and total organic C content of all plants (f) in June, July and August of 2014 in the burned and unburned plots on the lower and upper slopes. Bars mean standard errors. Different lowercase letters indicate significant differences of organic C content among the plots at P < 0.05 level in the same sampling month.

3.3 Effects of slope and spring fire on the N content of different plant functional groups

Slope positions and spring fire affected the N contents of C_3 grasses, forbs, C_4 grasses and total grasses in some of the sampling months (Fig. 4). The N content of C_4 grasses was significantly higher on the lower slope than on the upper slope in June (P<0.001; Fig. 4c). However, no significant differences were found between the lower and upper slopes in July and August. In July, there were significant differences in the N contents of C_3 grasses (P<0.01; Fig. 4a), A. frigida plants (P<0.05; Fig. 4d) and total grasses (P<0.01; Fig. 4e) in the unburned plots between the lower and upper slopes. Moreover, slope position did not significantly affect the total N content of all plants in the burned and unburned plots (P>0.05; Fig. 4f).

Spring fire had different effects on the N content of the different plant functional groups on the

lower and upper slopes in particular months (Fig. 4). On the lower slope, spring fire significantly decreased the N content of C_4 grasses in June (P < 0.001) and July (P < 0.05; Fig. 4c), and of A. frigida plants in July (P < 0.05) and August (P < 0.01; Fig. 4d). The N contents of C_3 grasses and total grasses were significantly (P < 0.01) higher in the burned plots than in the unburned plots on the upper slope in August (Figs. 4a and e). Spring fire significantly increased the N content of forbs (P < 0.05) and total N content of all plants (P < 0.01) in June and August (Figs. 4b and f).

ZHAO Xiang et al.: Effects of spring fire and slope on the aboveground biomass, and organic C and N...

On the upper slope, spring fire significantly increased the N contents of C_3 grasses (P<0.01; Fig. 4a) and total grasses (P<0.01; Fig. 4e) in July. No significant differences were found in the other plant functional groups between the burned and unburned plots during the growing season (P>0.05).

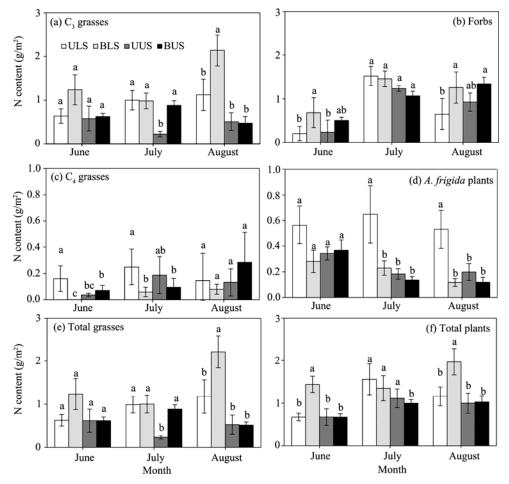


Fig. 4 N contents of C_3 grasses (a), forbs (b), C_4 grasses (c), A. frigida plants (d) and total grasses (e), and total N content of all plants (f) in June, July and August of 2014 in the burned and unburned plots on the lower and upper slopes. Bars mean standard errors. Different lowercase letters indicate significant differences of N content among the plots at P < 0.05 level in the same sampling month.

3.4 Interactive effects of sampling time, slope position and spring fire on the AGB and organic C and N contents

The sampling time (month), slope position and spring fire had different effects on the AGB (Table 1). Sampling time had a significant effect on the AGB of C_3 grasses (P < 0.05), C_4 grasses (P < 0.01), total grasses (P < 0.01) and forbs (P < 0.001) and the total AGB of all plants (P < 0.001). Slope position also showed a significant effect on the AGB of C_3 grasses (P < 0.001), total grasses (P < 0.001) and A. frigida plants (P < 0.05) and the total AGB of all plants (P < 0.001). Spring fire mainly exhibited a significant effect on the AGB of C_3 grasses (P < 0.05), total grasses (P < 0.05) and

A. frigida plants (P<0.01). There were significant interactive effects of sampling time and slope position on the AGB of C₃ grasses and C₄ grasses (P<0.05). Sampling time and spring fire interactively affected the AGB of forbs (P<0.05). Slope position and spring fire interactively and significantly affected the AGB of C₄ grasses and A. frigida plants (P<0.05). The interaction of sampling time, slope position and spring fire had a significant effect on the AGB of C₄ grasses (P<0.05).

Table 1 ANOVA results (F values) of the effects of sampling time (month), slope position, spring fire and their interactions on the aboveground biomass (AGB), organic carbon (C) and nitrogen (N) contents and the C/N ratio in different plant functional groups

		C ₃ grasses	C ₄ grasses	Total grasses	Forbs	A. frigida plants	Total plants
AGB	Time (T)	4.485*	5.422**	6.496**	14.728***	1.583	15.831***
	Slope (S)	21.477***	0.151	22.072***	0.026	6.422*	23.056***
	Fire (F)	5.358*	1.282	4.786*	1.818	9.796**	3.581
	$T \times S$	4.349*	3.385*	3.360^{*}	1.348	1.310	1.279
	$T \times F$	0.278	3.101	0.449	3.544*	0.465	2.957
	$S \times F$	0.769	5.519*	0.254	0.537	6.880^{*}	0.019
	$T{\times}S{\times}F$	3.195*	0.658	3.108	0.004	0.013	2.383
Organic C content	T	5.174**	8.261***	5.542**	16.065***	0.910	16.397***
	S	18.845***	1.257	11.396***	0.322	8.007***	23.808***
	F	3.541	2.350	0.680	3.814	8.279***	3.760
	$T \times S$	5.578**	2.607	4.369*	1.271	0.813	2.158
	$T \times F$	0.397	2.045	1.452	2.034	0.724	0.970
	$S \times F$	0.145	5.299*	0.038	0.374	5.374*	0.120
	$T{\times}S{\times}F$	2.226	0.220	1.471	0.017	0.035	1.911
N content	T	2.040	4.455*	2.599	8.537**	2.039	4.512*
	S	22.275***	0.590	21.626***	0.314	8.043**	12.086**
	F	7.949**	4.262*	7.648**	2.259	11.432**	2.671
	$T \times S$	3.403*	2.137	3.738*	1.779	1.034	0.180
	$T \times F$	0.233	3.890^{*}	0.188	2.251	0.384	2.146
	$S \times F$	1.248	9.740**	1.535	0.505	8.097**	3.521
	$T{\times}S{\times}F$	3.639*	0.437	3.183*	0.064	0.015	1.248
C/N ratio	T	19.327***	148.617***	50.386***	38.955***	10.616***	10.284***
	S	0.841	17.564***	1.361	0.573	3.424	0.150
	F	10.617**	21.439***	7.916**	0.118	3.278	1.349
	$T \times S$	3.162*	7.471**	2.130	2.987	1.261	4.816*
	$T \times F$	4.627*	13.347***	8.327**	0.172	0.276	2.353
	$S \times F$	2.302	0.003	0.922	0.063	9.336**	5.603*
	$T\times S\times F$	3.538*	47.316***	0.646	0.855	6.107**	0.969

Note: *, ** and *** represent significance at P<0.05, P<0.01 and P<0.001 levels, respectively.

Slope position, spring fire and sampling time had different interactive effects on the organic C and N contents and on the C/N ratio (Table 1). Sampling time significantly affected the organic C content and C/N ratio in all plant functional groups, with the exception of organic C content in A. frigida plants (P>0.5). Slope position and spring fire significantly interacted to affect the organic C and N contents of C₄ grasses (P<0.05 and P<0.01, respectively) and of A. frigida plants (P<0.05 and P<0.01, respectively). Spring fire had a marginal interaction with slope position, affecting the total N content of all plants at P<0.10 level. Sampling time, slope position and spring fire had a significant interactive effect on the organic N contents of C₃ grasses (P<0.05) and total grasses (P<0.05), and the C/N ratio of C₃ grasses (P<0.05), C₄ grasses (P<0.001) and A. frigida plants (P<0.01).

4 Discussion

4.1 Effects of slope position on the AGB and organic C and N contents

In this study, a higher total AGB was found on the lower slope than on the upper slope over three growing seasons from 2014 to 2016. The higher contents of soil moisture and nutrients may be attributed to the increased total AGB on the lower slope. The AGB of C₃ grasses and C₄ grasses showed different patterns on the lower and upper slopes. The AGB of C₃ grasses was higher on the lower slope than on the upper slope in all sampling months of 2014, while the AGB of C₄ grasses was higher on the upper slope than on the lower slope in August and in the burned plots in July of 2014. The reason for the difference in the AGB between C₃ and C₄ grasses on the lower slope was related to temperature at the regional and global scales (Epstein et al., 1997; White et al., 2008; Zhou et al., 2011). The C₄ grass species are usually distributed in warm regions whereas the C₃ grasses are preferred in cool regions (White et al., 2008), inducing a relative high AGB of C₄ grasses in the warmer plots. The temperatures are higher on the upper slope than on the lower slope in our study area, which resulted in the AGB of C₃ grasses being higher on the lower slope than on the upper slope.

In this study, spring fire contributed differently for C3 grasses and forbs on the upper and lower slopes. We observed a higher number of C₃ grasses and a lower number of forbs on the lower slope as opposed to a lower number of C₃ grasses and a higher number of forbs on the upper slope. The findings indicated that species composition differed between the lower and upper slopes because of soil physical-chemical properties and micro-environment. Liu et al. (2007) found large differences in the nutrient content of soils between the lower and upper slopes at another experimental site in northern China. Our result supports this finding. De Castilho et al. (2006) reported that soils from different topographies could explain almost one-third of the variation in the aboveground live biomass, suggesting that the AGB is affected by the nutrients in soils on the upper and lower slopes. However, topography can influence the hydrology or water redistribution (Gibson and Hulbert, 1987; Condon and Maxwell, 2015), as well as the vegetation (Burke et al., 1999; Jung et al., 2016, Shetie et al., 2017) on the slope. Soil temperature and moisture exhibited seasonal dynamics during the growing season in our study area. Soil moisture was always higher on the lower slope than on the upper slope during the study period (data not shown). Although a large part of the variation in the AGB remains unexplained, we still need some evidence that differences in the soil texture and fertility may affect the biomass accumulation on the upper and lower slopes.

In the study area, the dominant plant species differ between the upper (S. krylovii, A. frigida, G. pauciflora and C. squarrosa) and lower (L. chinensis, A. frigida and S. krylovii) slopes. The AGB was generally affected by the soil texture, which might be related to soil moisture, nutrient availability and nutrient cycling (Sariyildiz et al., 2005). Laurance et al. (1999) attributed the great spatial variation in the estimates of AGB to N availability. Plants are the source of nutrients and also serve as nutrient sinks by increasing the sequestration of nutrients when the supply of nutrients is adequate relative to the amount required for plant absorption. A significant difference between total soil N content and leaf N concentration at different topographical positions was observed in central Amazonia (Luizão et al., 2004). Fearnside and Leal Filho (2001) found that species characterized by large individuals were associated with a particular soil type, and this pattern was related to the biomass. The effect of soil on rare species could considerably affect the nutrient estimates of plants because only a few large individuals are needed to explain the large proportion of the AGB on a plot (Clark and Clark, 1996).

We found that slope position can also affect the dynamics of organic C and N contents of plants (Figs. 3 and 4) as well as the nutrient cycling (Luizão et al., 2004) in the semi-arid grasslands, which was consistent with the findings of Bellingham and Tanner (2000). In contrast to our results, the AGB estimated for meadow and tallgrass steppe grasslands was insensitive to the soil properties and/or topography (Turner et al., 1997).

4.2 Effects of spring fire on the AGB and organic C and N contents

The results of our study indicated that spring fire is beneficial for the biomass of C3 grasses and

forbs in the semi-arid grasslands to some degree, both of which may affect the grassland productivity and diversity of plants. On the one hand, the primary production of C_3 grasses and forbs following the spring fire was higher in the burned plots than in the unburned (control) plots on the lower slope in June and August of 2014. On the other hand, the higher litter production rates after fire burning may have further limited the regeneration of the grassland species, which resulted in a competitive advantage for some species, such as C_3 grasses and forbs (Whelan, 1995; Bond and Van Wilgen, 1996; Houghton et al., 2000).

Removing the aboveground parts in grasslands through fire can lead to a greater irradiance and an increase of evaporation from the soil surface (Knapp, 1984; Knapp and Seastedt, 1986). Hence, the surface energy balance of the ecosystem can be changed. The ecophysiology of plants (Knapp, 1985), species composition (Knapp, 1985; Gibson and Hulbert, 1987; Bachinger et al., 2016; Heydari et al., 2016), and aboveground productivity (Knapp, 1984; Hulbert, 1988; D'Antonio and Mack, 2006) can be changed by the fire. We did not find any change in the species composition in our experiment. However, in 2014 and 2015, the total AGB increased because of spring fire, i.e., the total AGB was higher in the burned plots than in the unburned plots. Briggs and Knapp (1995) found that the aboveground productivity was 102 g/m² higher in the burned lowlands than in the unburned ones in a tallgrass prairie over a period of 18 years.

In our study, there were no significant increases in the AGB of all plant functional groups on the lower slope after the spring fire treatment during the growing season of 2014, with the only exception of forbs. Spring fire decreased the AGB of C₄ grasses and A. frigida plants on the lower slope, while increased the AGB of C₃ grasses and total grasses. On the upper slope, spring fire increased the AGB of C₄ grasses in July. These results demonstrated that C₄ grass species prefer high temperatures than C₃ grass species do. We also found that spring fire could increase the N contents of C₃ grasses and total plants whereas decrease the N contents of C₄ grasses and A. frigida plants on the lower slope. Our results are supported by the findings of Brys et al. (2005) that fire burning could increase the leaf N content of Molinia caerulea. Previous studies in temperate grasslands suggested that fire may exacerbate N limitation when it is very frequent (Seastedt et al., 1991; Ojima et al., 1994; Knapp et al., 1998). However, in our study, spring fire did not decrease the N content. The difference might be caused by the experiment duration in different studies.

We observed that spring fire significantly increased the N content of forbs only on the lower slope. This may be due to the fire possibly increased the forb diversity in N-limited systems by benefiting N-limited legumes, which increased the N availability in the soil (Dudley and Lajtha, 1993). Similar results were also reported by Van Dyke et al. (2007), who found that fire burning treatment only added one legume species to the tallgrass prairies and that most of the burned sites contained only five C₄ grass species, which might benefit from an early spring fire.

5 Conclusions

In the present study, we found that spring fire on different slope positions significantly affected the AGB of different plant functional groups (C₃ grasses, C₄ grasses, forbs, *A. frigida* plants, total grasses and total plants) after the spring fire in 2014. The total AGB was higher on the lower slope than on the upper slope, which was caused by the presence of different species in the different plots as well as higher soil moisture content and more nutrient supply on the lower slope. A similar trend was observed for the organic C and N contents. The interactive effects between slope position and spring fire on the AGB and organic C and N contents were dependent on the months of the growing season. Based on the results, we conclude that spring fire can improve the productivity and nutrient content of grasslands. Thus, we recommend spring fire to be a management strategy to sustainably protect the grasslands.

Acknowledgements

This study was partially supported by the National Key Basic Research and Development Program of China (2016YFC0500703) and the National Natural Science Foundation of China (31572452, 41573063, 31870438).

References

- Abrams M D, Hulbert L C. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. American Midland Naturalist, 117(2): 442–445.
- Bachinger L M, Brown L R, van Rooyen M W. 2016. The effects of fire-breaks on plant diversity and species composition in the grasslands of the Loskop Dam Nature Reserve, South Africa. African Journal of Range & Forage Science, 33(1): 21–32.
- Barbosa R I, Fearnside P M. 2005. Above-ground biomass and the fate of carbon after burning in the savannas of Roraima, Brazilian Amazonia. Forest Ecology and Management, 216(1–3): 295–316.
- Bellingham P J, Tanner E V J. 2000. The influence of topography on tree growth, mortality, and recruitment in a tropical Montane Forest. Biotropica, 32(3): 378–384.
- Bennie J B, Hill M O, Baxter R, et al. 2006. Influence of slope and aspect on long-term vegetation change in British chalk. Journal of Ecology, 94(2): 355–368.
- Benning T L, Seastedt T R. 1995. Landscape-level interactions between topoedaphic features and nitrogen limitation in tallgrass prairie. Landscape Ecology, 10(6): 337–348.
- Blair J M. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecology, 78(8): 2359–2368.
- Bond W J, Van Wilgen B W. 1996. Fire and Plants. London: Chapman and Hall Press, 42–46.
- Briggs J M, Knapp A K. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. American Journal of Botany, 82(8): 1024–1030.
- Brys R, Jacquemyn H, De Blust G. 2005. Fire increases aboveground biomass, seed production and recruitment success of *Molinia caerulea* in dry heathland. Acta Oecologica, 28(3): 299–305.
- Burke I C, Lauenroth W K, Riggle R, et al. 1999. Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems, 2(5): 422–438.
- Cabrera M L, Beare M H. 1993. Alkaline persulfate oxidation for determining total nitrogen in microbial biomass extracts. Soil Science Society of America Journal, 57(4): 1007–1012.
- Cianciaruso M V, da Silva I A, Batalha M A. 2010. Aboveground biomass of functional groups in the ground layer of savannas under different fire frequencies. Australian Journal of Botany, 58(3): 169–174.
- Clark D B, Clark D A. 1996. Abundance, growth and mortality of very large trees in neotropical lowland rain forest. Forest Ecology and Management, 80(1–3): 235–244.
- Condon L E, Maxwell R M. 2015. Evaluating the relationship between topography and groundwater using outputs from a continental-scale integrated hydrology model. Water Resources Research, 51(8): 6602–6621.
- Corre M D, Schnabel R R, Stout W L. 2002. Spatial and seasonal variation of gross nitrogen transformations and microbial biomass in a northeastern US grassland. Soil Biology and Biochemistry, 34(4): 445–457.
- D'Antonio C M, Mack M C. 2006. Nutrient limitation in a fire-derived, nitrogen-rich Hawaiian grassland. Biotropica, 38(4): 458-467.
- De Castilho C V, Magnusson W E, de Araújo R N O, et al. 2006. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. Forest Ecology and Management, 234(1–3): 85–96.
- Dudley J L, Lajtha K. 1993. The effects of prescribed burning on nutrient availability and primary production in sandplain grasslands. American Midland Naturalist, 130: 286–298.
- Epstein H E, Lauenroth W K, Burke I C, et al. 1997. Productivity patterns of C₃ and C₄ functional types in the U.S. Great Plains. Ecology, 78(3): 722–731.
- Fearnside P M, Leal Filho N. 2001. Soil and development in Amazonia: lessons from the biological dynamics of forest fragment project. In: Bierregaard J O R, Gascon C, Lovejoy T E, et al. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. New Haven: Yale University Press, 291–312.
- Gibson D J, Hulbert L C. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio, 72(3): 175–185.
- Guo Q F. 2001. Early post-fire succession in California chaparral: Changes in diversity, density, cover and biomass. Ecological Research, 16(3): 471–485.
- Hartnett D C, Hickman K R, Walter L E F. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Journal of Range Management, 49(5): 413–420.
- Heydari M, Faramarzi M, Pothier M. 2016. Post-fire recovery of herbaceous species composition and diversity, and soil quality indicators one year after wildfire in a semi-arid oak woodland. Ecological Engineering, 94: 688–697.
- Hook P B, Burke I C. 2000. Biogeochemistry in a shortgrass landscape: control by topography, soil texture, and microclimate.

- Ecology, 81(10): 2686-2703.
- Houghton R A, Hackler J L, Lawrence K T. 2000. Changes in terrestrial carbon storage in the United States. 2: The role of fire and fire management. Global Ecology & Biogeography, 9: 145–170.
- Hulbert L C. 1988. Causes of fire effects in tallgrass prairie. Ecology, 69(1): 46-58.
- Jung G, Prange M, Schulz M. 2016. Influence of topography on tropical African vegetation coverage. Climate Dynamics, 46(7–8): 2535–2549.
- Kaye T N, Pendergrass K L, Finley K, et al. 2001. The effect of fire on the population viability of an endangered prairie plant. Ecological Applications, 11(5): 1366–1380.
- Knapp A K. 1984. Post burn differences in solar radiation leaf temperature and water stress influencing production in a lowland tall grass prairie. American Journal of Botany, 71(2): 220–227.
- Knapp A K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. Ecology, 66(4): 1309–1320.
- Knapp A K, Seastedt T R. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience, 36(10): 662-668.
- Knapp A K, Conard S K, Blair J M. 1998. Determinants of soil CO₂ flux from a sub-humid grassland: effect of fire and fire history. Ecological Applications, 8(3): 760–770.
- Laurance W F, Fearnside P M, Laurance S G, et al. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. Forest Ecology and Management, 118(1–3): 127–138.
- Lavian I L, Vishneretsky S, Barness G, et al. 2001. Soil microbial community and bacterial functional diversity at Machu Picchu, King George Island, Antarctica. Polar Biology, 24(6): 411–416.
- Liu W X, Xu W H, Han Y, et al. 2007. Responses of microbial biomass and respiration of soil to topography, burning, and nitrogen fertilization in a temperate steppe. Biology and Fertility of Soils, 44(2): 259–268.
- Luizão R C C, Luizão F J, Paiva R Q, et al. 2004. Variation of carbon and nitrogen cycling processes along a topographic gradient in a Central Amazonian forest. Global Change Biology, 10(5): 592–600.
- Ma W H, He J S, Yang Y H, et al. 2010. Environmental factors covary with plant diversity-productivity relationships among Chinese grassland sites. Global Ecology and Biogeography, 19(2): 233–243.
- Menges E S, Quintan-Ascencio P F. 2004. Population viability with fire in *Eryngium cuneifolium*: Deciphering a decade of demographic data. Ecological Monographs, 74(1): 79–99.
- Moreira A G. 2000. Effects of fire protection on savanna structure in Central Brazil. Journal of Biogeography, 27(4): 1021-1029.
- Morrison D A. 2002. Effects of fire intensity on plant species composition of sandstone communities in the Sydney region. Austral Ecology, 27(4): 433–443.
- Ojima D S, Schimel D S, Parton W J, et al. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry, 24(2): 67–84.
- Reynolds H L, Mittelbach G G, Darcy-Hall T L, et al. 2007. No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. Journal of Ecology, 95(4): 723–733.
- Riihimäki H, Heiskanen J, Luoto M. 2017. The effect of topography on arctic-alpine aboveground biomass and NDVI patterns. International Journal of Applied Earth Observation and Geoinformation, 56: 44–53.
- Röver M, Kaiser E A. 1999. Spatial heterogeneity within the plough layer: low and moderate variability of soil properties. Soil Biology and Biochemistry, 31(2): 175–187.
- Rowe J S. 1984. Forestland classification: limitations of the use of vegetation. In: Bockheim J G. Forestland Classification: Experiences, Problems, Perspectives. Madison: Department of Soil Science, 132–148.
- Safford H D, Harrison S. 2004. Fire effects on plant diversity in serpentine vs. sandstone chaparral. Ecology, 85(2): 539-548.
- Saito M, Luyssaert S, Poulter B, et al. 2014. Fire regimes and variability in aboveground woody biomass in miombo woodland. Journal of Geophysical Research-Biogeosciences, 119(5): 1014–1029.
- Sariyildiz T, Anderson J M, Kucuk M. 2005. Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. Soil Biology and Biochemistry, 37(9): 1695–1706.
- Satterthwaite W H, Menge E S, Quintana-Ascencio P F. 2002. Assessing scrub buckwheat population viability in relation to fire using multiple modeling techniques. Ecological Applications, 12(6): 1672–1687.
- Schaffers A P. 2002. Soil, biomass, and management of semi-natural vegetation. Plant Ecology, 158(2): 247–268.
- Seastedt T R, Briggs J M, Gibson D J. 1991. Controls of nitrogen limitation in tallgrass prairie. Oecologia, 87(1): 72-79.
- Shaukat S S, Hussain F, Zafar H, et al. 2014. Species composition, spatial heterogeneity, interspecific association and diversity of an early successional plant community: A comparison of some species association indices. International Journal of Biology and Biotechnology, 11(4): 677–691.
- Shetie G M, Dondeyne S, Nyssen J, et al. 2017. Elucidating woody vegetation patterns in relation to soil and topography in

- tropical Africa: the case of Nech Sar National Park (Ethiopia). Plant Ecology and Evolution, 150: 45–58.
- Tilman D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation. Ecology, 74(8): 2179–2191.
- Turner C L, Blair J M, Schartz R J, et al. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. Ecology, 78(6): 1832–1843.
- Van Dyke F, Schmeling J D, Starkenburg S, et al. 2007. Responses of plant and bird communities to prescribed burning in tallgrass prairies. Biodiversity and Conservation, 16(4): 827–839.
- Vargas R, Allen M F, Allen E B. 2008. Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical forest. Global Change Biology, 14(1): 109–124.
- Vijayakumar D B I P, Raulier F, Bernier P, et al. 2016. Cover density recovery after fire disturbance controls landscape aboveground biomass carbon in the boreal forest of eastern Canada. Forest Ecology and Management, 360: 170–180.
- Vitousek P M, Turner D R, Parton W J, et al. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms, and models. Ecology, 75(2): 418–429.
- Wahren C H A, Papst W A, Williams R J. 2001. Early post-fire regeneration in subalpine heathland and grassland in the Victorian Alpine National Park, south-eastern Australia. Austral Ecology, 26(6): 670–679.
- Wan S Q, Hui D F, Luo Y Q. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecological Applications, 11(5): 1349–1365.
- Whelan R J. 1995. The Ecology of Fire. Cambridge: Cambridge University Press, 112-124.
- White T A, Campbell B D, Kemp P D, et al. 2008. Impacts of extreme climatic events on competition during grassland invasions. Global Change Biology, 7(1): 1–13.
- Xu W H, Wan S Q. 2008. Water-and plant-mediated responses of soil respiration to topography, fire, and nitrogen fertilization in a semiarid grassland in northern China. Soil Biology and Biochemistry, 40(3): 679–687.
- Zhou X, Ge Z M, Kellomaki S, et al. 2011. Effects of elevated CO₂ and temperature on leaf characteristics, photosynthesis and carbon storage in aboveground biomass of a boreal bioenergy crop (*Phalaris arundinacea* L.) under varying water regimes. Global Change Biology Bioenergy, 3(3): 223–234.